

Diversity emerging: from competitive exclusion to neutral coexistence in ecosystems

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Abstract In this communication, we present a unifying framework to understand the emergence and maintenance of diversity in ecological systems. We do this by developing a deterministic population model including density-dependent limitation in resources and available space. Our model shows that competitive exclusion and neutral coexistence represent different regimes of the same adaptive dynamics suggesting that neutrality is the general result of an adaptive process in a finite habitat with limited energetic resources. Our model explains the emergence of biodiversity through mutation and its maintenance through neutrality. We show that this framework provides the theoretical foundations to

understand the emergence and maintenance of diversity in microbial ecosystems.

Keywords Emergence · Diversity · Adaptive dynamics · Competition · Neutrality

Introduction

The processes by which diversity is generated and maintained in ecosystems are at the core of ecological inquiry. And yet, it is striking that we do not have a simple and general quantitative theory of biodiversity generation and maintenance, notwithstanding several recent efforts in this direction (Hubbell 1997, 2001; Huisman et al. 2001; Allen et al. 2002; Brown et al. 2004). One of the impediments for achieving a general theory is the fondness of ecologists with complex ecological systems

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such as tropical forests and coral reefs, as if a general theory of biodiversity should be easier to achieve under the inspiration of highly diverse ecosystems, e.g., Volkov et al. (2007). In this context, it is not surprising that most theories, such as neutral and stochastic theories as well as niche and resource-based ones (Hubbell 1997, 2001; Caswell 1976; Tilman 1982, 1994; Chesson 2000; Tilman and Pacala 1993) emphasize biodiversity maintenance but lack a formal treatment of biodiversity generation. In contrast, simple ecosystems represented by cultured bacteria populations, by virtue of their large population size, short generation time, and easy of experimentation, have gradually taken a leading role in fostering our understanding of the processes underlying the emergence of diversity (Rainey et al. 2000; Seehausen 2007).

It is well known that cultures inoculated with an isogenic strain of bacteria gradually give rise to diversity, or genetic polymorphism in the form of mutant strains, even in the absence of environmental heterogeneity, e.g., Zambrano et al. (1993), Rosenzweig et al. (1994), Riley et al. (2001), and Maharjan et al. (2006). Typically, population takeovers by fitter mutants (i.e., periodic selection, Atwood et al. 1951) have been the rule in chemostat (Novick and Szilard 1951; Helling et al. 1987) and in serial transfer batch cultures (Lenski and Travisano 1994). Periodic selection is closely associated with competitive exclusion and thus with the winning and complete takeover by the fittest mutant. Chemostats and sequential transfer experiments, however, may not adequately represent all extant diversity due to potential losses accrued by dilution (as in chemostats) or by transferring only a sample of the population to a fresh medium (as in sequential transfer lines). Furthermore, the usual culturing conditions might not adequately represent the stress associated to low resource levels and intense competition, which are common in natural microbial ecosystems (Morita 1988, 1997; Zinser and Kolter 2004; Finkel 2006), and the increased mutation rate and diversity that these may trigger (Bjedov et al. 2003; Tenaillon et al. 2004). In fact, experimental results on bacterial evolution under stress conditions (i.e. batch cultures with prolonged starvation, Zambrano et al. 1993; Finkel and Kolter 1999; Zinser and Kolter 1999, 2000) not only resulted in the commonly observed periodic selection but also in high levels of strain diversity (see Fig. 1). Interestingly, while it was early recognized that these result could hold important insights for understanding the mechanisms underlying the emergence of diversity in ecosystems (Finkel 2006; Finkel and Kolter 1999), see reviews in Zinser and Kolter (2004), no theory has explained them as yet.

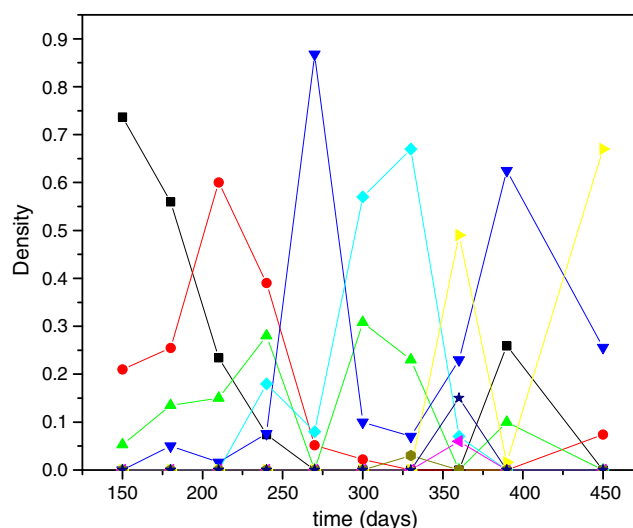


Fig. 1 Coexistence of different colony morphotypes, indicated by colors, during long-term incubation of an initially isogenic strain of *E. coli*. From data in Fig. 4 of Finkel and Kolter (1999)

In this paper, we present a general model to understanding the emergence and maintenance of diversity in ecological systems, which uses exploitative competition for resources (Tilman 1982; Hansen and Hubbell 1980; Finkel et al. 2000), in an adaptive dynamics framework. Our central tenet is that diversity is driven by two density-dependent mechanisms: spatial constraints to individual packing and resource constraints to individual persistence and reproduction. Our model shows that the interaction between these two limiting factors underlies biodiversity generation through mutation (innovation) and maintenance through neutrality. Furthermore, we show that this framework provides the theoretical foundations for understanding the emergence and maintenance of diversity in microbial ecosystems.

The model

Following Keymer et al. (2006), we consider a logistic Verhulst-type growth scenario

$$\frac{d}{dt}\phi = r\phi(1 - \phi), \quad (1)$$

where ϕ is the biomass of the bacterial strain. The logistic term in this equation represents the effect of the finiteness of the habitat wherein resources and biomass are contained, such that even if resources to provision further growth are present, this will not occur because of lack of space to put new biomass.

We assume that the growth rate r depends on the quality of the habitat ω , $0 \leq \omega \leq 1$, which specifies the amount of local resources that can be turned into new biomass. Then,

$$r(\omega) = f\omega - m, \quad (2)$$

with f and m being fecundity and mortality rates, respectively. Habitat-quality dynamics is modeled as

$$\frac{d}{dt}\omega = F - C, \quad (3)$$

where F and C are the supply and consumption rates of resources, respectively. We model them using the following functional forms

$$F = \lambda(1 - \omega), \quad C = \epsilon\phi\omega f, \quad (4)$$

where λ is the supply rate of resources while ϵ represents the amount of nutrients per unit biomass. This formulation comes from the resource-based model introduced by Roughgarden (1998).

The scenario we are interested corresponds to a strain growing in a habitat that do not receive any external supply of resources after colonization, as in Kolter's bacterial batch culture, but where new resources become available from the inside as a result of biomass decomposition or as by-products of the metabolic activity of bacteria, through the process known as cross-feeding, e.g., Helling et al. (1987). Notice that, in our model, negative density dependence acts upon fecundity as well as mortality, such that when biomass saturates the habitat, reaching stationary phase, both rates tend to zero. This is a well-known phenomena in bacterial cultures, where upon reaching stationary-phase bacterial cells cease to grow and divide, entering metabolic arrest or a spore-like physiological state; surviving for long periods of time with minimal metabolic activity (Kolter et al. 1993; Vulić and Kolter 2001).

By using Eqs. 1 and 3 we represent such ecology as

$$\frac{d}{dt}\phi = (f\omega - m)\phi(1 - \phi), \quad (5)$$

$$\frac{d}{dt}\omega = \lambda(1 - \omega) - \epsilon\phi\omega f. \quad (6)$$

This system has three possible long-term behaviors (indicated with supra-indices):

- Extinction. In this scenario, biomass goes to zero $\hat{\phi}^0 = 0$. However, due to the resources supplied by the biomass through its metabolic activity, the habitat quality goes to its maximum $\hat{\omega}^0 = 1$ (i.e., the habitat is saturated with resources accumulated as a by-product of metabolism).

- Bottom-up regulated. Here, we have that biomass in the long-term goes to $\hat{\phi}^{1/2} = \lambda(R - 1)/(f\epsilon)$, where $R = 1/\omega^*$ and $\omega^* = m/f$ while habitat quality goes to $\hat{\omega}^{1/2} = \omega^*$.
- Top-down regulated. Here, biomass reach a maximum saturating the habitat, $\hat{\phi}^1 = 1$ while habitat quality goes to $\hat{\omega}^1 = H$, with $H = \lambda/(\lambda + \epsilon f)$.

If we normalize time as $1/f$, we arrive to the following simplified equations

$$\frac{d}{d\tau}\phi = (\omega - \omega^*)\phi(1 - \phi), \quad (7)$$

$$\frac{d}{d\tau}\omega = \frac{\lambda}{f}(1 - \omega) - \epsilon\phi\omega. \quad (8)$$

Here, we assume that $\epsilon > 0$ and the resource recycling through cross-feeding $\lambda > 0$ are both fixed, and that the trait ω^* ($\omega^* = m/f$) is subject to an adaptive dynamics, whereby new mutant strategies characterized by slight changes in ω^* continuously arise in the population (see next section below).

As before there are three equilibrium points. The extinction equilibrium is stable when a strategy is characterized by $\omega^* > 1$ (i.e., mortality is higher than fecundity). The bottom-up regulated equilibrium is stable for strategies satisfying $H < \omega^* < 1$. As strategies with smaller ω^* are considered, the top-down regulated equilibrium will kick in. This last equilibrium, $\hat{\omega}^1 \equiv H$, is stable when $0 \leq \omega^* \leq H$ that is, when resources are no longer constraining biomass accumulation. At this point, the finite nature of the habitat becomes a strong constraint upon new biomass, as there is no more free volume to put the new biomass that can be made. Here, habitat quality is determined by the parameters λ and ϵ .

In general, the important parameters for the stability of the system are ω^* , which measures the ratio between mortality and fecundity, and $\epsilon f/\lambda$, that appears in the threshold H . Figure 2 shows the stationary solutions for the equilibrium biomass $\hat{\phi}$ and their stability properties.

To understand the dynamic implications of this phenomenon, in an environment where new mutants may continually arise, we now turn to an adaptive dynamics framework (e.g. Metz et al. 1996; Diekmann 2004).

Adaptive dynamics

An adaptive dynamics in a continuous trait space is particularly suited for uncovering the most likely course that evolution would follow under the conditions

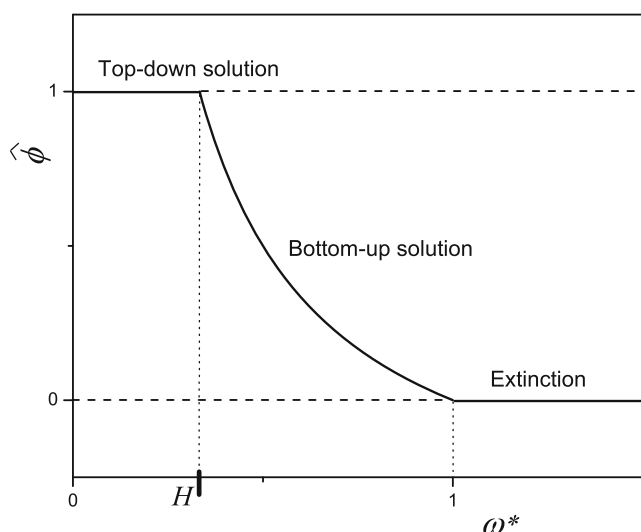


Fig. 2 Equilibrium states for the dynamics of biomass in a patch with resource renewal. *Continuous* and *dashed lines* represent stable and unstable equilibria, respectively

specified by our deterministic model (Metz et al. 1996; Diekmann 2004).

Two of the fundamental ideas of adaptive dynamics are: (1) that a resident population, ϕ_r , can be assumed at equilibrium $\phi_r \equiv \hat{\phi}_r$ when new mutants, ϕ_μ , appear and that (2) the fate of these mutants can be inferred from their growth rate when rare (i.e., at the beginning of the invasion) in the environment occupied by the resident, this per capita rate is defined below and it is known as the invasion exponent S or invasion fitness (Metz et al. 1992). Finally, we calculate the selection gradient S' which gives a local description of the fitness landscape experienced by an emerging (rare) mutant, indexed by μ , in the context of an equilibrium resident population, indexed by r (Diekmann 2004), under the ecological conditions described by Eqs. 7 and 8.

Notice that applying adaptive dynamics theory for this case is straightforward (see Online Resource 1), and we only need to consider the change in attractor stability when the evolving trait crosses a critical boundary, triggering a stability change in the fixed points for the resident population. In general, we need to perform an invasion analysis for each of the three regions of the parameters space, which correspond to attractors $\hat{\phi}^0$, $\hat{\phi}^{1/2}$, or $\hat{\phi}^1$.

Since in order to evolve, strategies must actually exist, we know that the relevant problem only involve strategies in the region $0 \leq \omega^* < 1$. So, only two cases must be considered as our equilibrium resident population $\hat{\phi}_r$: (a) bottom-up $\hat{\phi}_r^{1/2}$ scenario for strategies $H < \omega^* < 1$, and (b) a top-down $\hat{\phi}_r^1$ scenario for strategies $0 \leq \omega^* \leq H$.

In both cases, we consider the fate (invasion exponent) of a rare strategy ω_μ^* , defined by

$$S \equiv S_{\omega_r^*}(\omega_\mu^*) \equiv \frac{1}{\phi_\mu} \frac{d}{d\tau} \phi_\mu = (\omega_r^* - \omega_\mu^*) (1 - \hat{\phi}_r), \quad (9)$$

within a background environment characterized by an equilibrium resident strategy ω_r^* resting at its (stable) equilibrium point $\hat{\phi}_r$ (see Online Resource 1).

The particular equilibrium point ($\hat{\phi}_r^{1/2}$ or $\hat{\phi}_r^1$) to consider for the resident equilibrium density $\hat{\phi}_r$, depends on what region of the strategy space is the resident trait ω_r^* at.

Case I, $H < \omega_r^* < 1$. Corresponds to the bottom-up regulated equilibrium. Thus, $\hat{\phi}_r^{1/2}$ ought to be considered. For this case the invasion exponent corresponds to:

$$S = (\omega_r^* - \omega_\mu^*) (1 - \hat{\phi}_r^{1/2}), \quad (10)$$

and the fitness gradient for the mutants looks like

$$S' \equiv \frac{d}{d\omega_\mu^*} S_{\omega_r^*} = \hat{\phi}_r^{1/2} - 1, \quad (11)$$

which is negative, $S' < 0$ since $\hat{\phi}_r^{1/2} < 1$. Thus, there is a directional evolution of the trait ω^* to the left (smaller values) in strategy space until it reaches strategies within the next region, to the left of $\omega_c^* \equiv H$.

Case II, $0 \leq \omega_r^* \leq H$. Corresponds to strategies that saturate available space. For these strategies, the equilibrium point to consider corresponds to the top-down

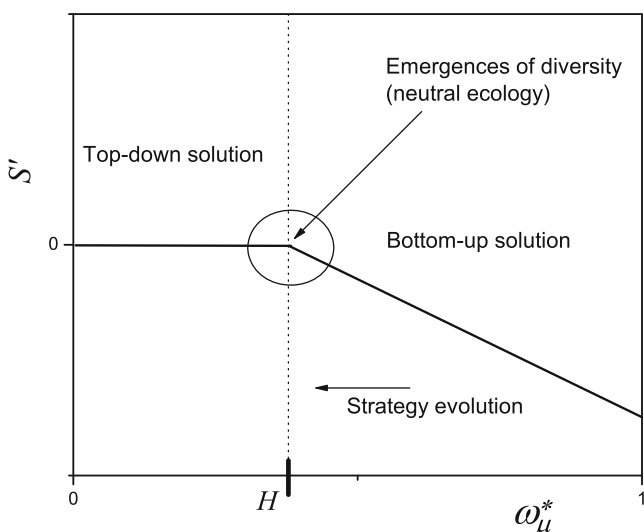


Fig. 3 Selection gradient as a function of ω^* . The threshold value H , is where the top-down solution becomes stable. This is the boundary at which a neutral ecology emerges

regulated one $\hat{\phi}_r \equiv \hat{\phi}_r^1 = 1$. In this case, the invasion exponent of any new mutant vanishes, since

$$S = (\omega_r^* - \omega_\mu^*) (1 - \hat{\phi}_r^1) = 0. \quad (12)$$

A plot of the selection gradient, S' , associated to the bottom-up equilibrium is negative, implying a steep fitness landscape where new mutant strategies carry a selective advantage over the resident one, and thus can invade the population (Fig. 3). However, as soon as the bottom-up regulated equilibrium is reached the invasion exponent of any new mutant vanishes and as a consequence the fitness gradient becomes flat and a neutral ecology emerges, where any possible mutant that arises is ecologically equivalent.

Discussion

Ever since the struggle for existence and the competitive exclusion principle, diversity, and more generally coexistence, has been a vexing problem in ecology and evolutionary biology (Muller 1932).

Spontaneous beneficial mutations are the fundamental source for adaptation, innovation and diversity. In asexual populations, however, mutants better endowed with fitness will tend to replace other mutants through periodic selection or clonal interference (Gerrish and Lenski 1998; Hegreness et al. 2006) putting a ceiling to diversity at its lowest value. Several hypothesis and models based on resource partitioning, cross-feeding, demographic trade-offs, and frequency-dependent selection have envisioned realistic scenarios for fitness equalization and thus coexistence and microbial diversity (Rosenzweig et al. 1994; Helling et al. 1987; Turner et al. 1996; Rozen and Lenski 2000; Czárán et al. 2002; Kerr et al. 2002; Friesen et al. 2004) with the recently proposed neutral theory (Hubbell 2001) representing an extreme explanation, which assumes that individuals live in a flat fitness landscape, such that diversity is driven by mutation, dispersal and ecological drift (Hubbell 2001).

Our model builds on resource-based competition, which when taking place in a finite habitat gives way to neutrality as a result. It unifies both approaches by assuming that species, in addition of being limited by resources (our bottom-up regulation) also face the geometric constraints imposed by the finiteness of their habitats (our top-down constraint), when packing biomass into individuals. The combined action of these density-dependent effects gives raise to an adaptive dynamics characterized by a transition from fitness-

mediated competitive exclusion to neutrality. The later arises when the habitat patch is saturated with biomass, such that any new favorable mutation, let say for using a different amino acid as a source of carbon, is not better endowed than any other one. This result is equivalent to the biotic saturation or zero-sum assumption in first-generation neutral models (Hubbell 2001). In this regard, what our model shows is that space limitation is sufficient to put the dynamics of species diversity, as driven by competition and speciation, into a flat fitness landscape or neutral regime. In this sense, space limitation provides a hard boundary that equalizes fitness by not allowing room for new and better adapted varieties. Recent neutral models have relaxed the zero-sum assumption but have retained the neutrality or symmetry assumption that all individuals behave the same under the same intraspecific circumstances (Alonso et al. 2008; Haegeman and Etienne 2008) in order to derive observables such as abundance distributions. Our model is fundamentally different in this regard, as we do not assume neutrality but arrive to it through an adaptive dynamics driven by food and space limitation. In this sense, it is similar to recent models where neutrality is the result of ecological equivalence driven by mechanisms that equalize fitness (e.g., life-history trade-offs and dispersal limitation) and therefore allows for the coexistence of different types in competitive communities (Bonsall et al. 2004; Gravel et al. 2006; Scheffer and van Nes 2006; Doncaster 2009). It differs from them, however, in that the main forces driving diversity and coexistence are limitation for energy resources and space, while not assuming species specific trade-offs in competitive abilities or dispersal. It remains to be explored how the neutral dynamics resulting from our model compares with predictions derived from neutral models, such as species abundance distributions and other observables (Etienne and Alonso 2005).

Our model captures the essential features of the long-term starvation experiments that inspired its development (Finkel and Kolter 1999), that is, waves of successive takeovers or periodic selection followed by coexistence of multiple mutants. The mechanisms underlying the emergence of progressively fitter mutants that get a growth advantage in stationary phase (i.e., that possess the GASP phenotype), with a competitive advantage to mutants of order $n + 1$ over those of lower order (i.e., that emerged earlier in the population), is related to several GASP mutations (Zambrano et al. 1993; Zinser and Kolter 2004; Zinser and Kolter 1999, 2000) which, among other things, result in an increased ability to catabolize one or more amino acids as a source of carbon and energy.

The ecological scenario of a batch cultured population of *Escherichia coli* entering GASP (around 10 days after initial inoculation) is characterized by the nearly exhaustion of carbon sources from where to extract energy, unless new mutations allow for the use of the only carbon sources available; organic compounds derived from metabolic activity and those trapped in bacterial biomass. Once a GASP mutant arises, it will take over the population only to be replaced by mutants more efficient in using other available sources of carbon, scavenging for the carbon retained in the debris of dead bacterial cells or both. Indeed, in Zinzer and Kolter (1999) it is shown that GASP mutations act additively, conferring faster growth on mixtures of amino acids. During the neutral phase, all resources have been transformed to bacterial biomass, which becomes the resource itself. During this stage, it is possible to hypothesize that fitness will no longer increase after all the mutations required to use available amino acids have occurred, putting the dynamics onto a flat fitness landscape where bacterial biomass becomes the consumer and the resource. In this sense, our density-dependent constraint linked to habitat size somehow impose a limit to adaptation. It is also possible that successive strains are engaged in niche construction dynamics (Odling-Smee et al. 2003) such that although they may exclude each other, the winner always change the selective environment to favor a new variety until no further construction is possible. The functioning of this neutral ecosystem will slowly degrade in time as a consequence of energy dissipation, causing biomass to decrease. So far, long-term starvation experiments of bacteria have lasted for more than 5 years, and although there is evidence of a biomass decrease, see Fig. 1 in Finkel (2006), further analyses are necessary.

Finally, it is important to point out that resource and geometric constraints due to habitat finiteness are simple but fundamental ubiquitous characteristics of life, present since its emergence on earth. The model proposed herein derives how under these constraints competitive exclusion, diversity and neutrality can arise. Furthermore, our model suggests that neutrality may not only be an assumption for mathematical tractability or a null model for ecological understanding (Hubbell 2001; Caswell 1976; Alonso et al. 2006) but the general results of an adaptive process in a finite habitat with limited resources.

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